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High fidelity preservation of fossil insects from the Crato Formation (Lower Cretaceous) of Brazil

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ABSTRACT

Fossil insects from the Lower Cretaceous (Aptian) Crato Formation of north-east Brazil are preserved as goethite replacements in laminated limestones of lacustro-lagoonal origin. They display remarkable degrees of morphological detail down to the macro molecular level in some examples. We document the fidelity of preservation and reveal a remarkable variety of morphological detail comparable in some instances with that found in amber inclusions.

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1. Introduction

The Crato Formation represents one of the richest Cretaceous fossil Konservat-Lagerstätten in the world, yielding an exceptionally well preserved and diverse palaeobiota (Martill et al., 2007a). Although the formation yields abundant vertebrates, including rare dinosaurs, crocodiles and abundant pterosaurs and fishes, it also preserves diverse crustaceans, arachnids, and plants. However, it is perhaps most famous for the astonishing diversity and remarkable preservation of its fossil insects (Grimaldi, 1990; Martill et al., 2007a; Heads et al., 2008).

The insects of the Crato Formation are extremely important to our understanding of insect evolution for a number of reasons. Importantly, their Late Aptian (Early Cretaceous) age coincides with a time at which angiosperms were diversifying (Hochuli et al., 2006) and developing the complex relationships with insects that so strongly influenced their subsequent evolution and characterizes their biology to this day. In addition, with other fossils, the overall assemblage provides a unique glimpse of an ancient biota that existed at this time. Understanding the development of these relationships is vital to understanding not only the Mesozoic record of plant-insect interactions but ultimately, the structure and stability of modern terrestrial ecosystems. Furthermore, the Crato Formation is the only well-documented insect Lagerstätte of its age from Gondwana, representing an extremely valuable source of data concerning diversification and austral biogeography during one of the most complex continent scale vicariance events in insect history.

The Crato Formation boasts an extremely high diversity and abundance of fossil insects, with at least 15 different orders represented and over 350 named species described. In addition, many families are represented by as yet unnamed taxa (Bechly, 2007, 2010; Staniczek et al., 2011). These fossils are preserved exceptionally well, with details visible at the micron and sometimes nanometre scale. Despite this little is known about the processes of preservation and the quality of preservation is often under-reported in species descriptions.

Here we illustrate the exceptional quality of preservation displayed by the Crato Formation insects, describe the preservational fabrics, and suggest possible conditions that result in such preservation.

2. Locality and Geological Background

The Crato Formation crops out on the northern flanks of the Chapada do Araripe, a ~150km east-west plateau, located on the borders of the north-east Brazilian states of Ceará, Pernambuco and Piauí (Fig. 1). The formation is mined extensively for commercial purposes in the vicinity of Santana do Cariri and Nova Olinda in Ceará, and it is from these areas that most fossils are obtained.

The formation itself is a ~60m thick heterolithic sequence dominated in its middle part by laminated limestones, interbedded at their base with claystones, siltstones, and sandstones (Heimhofer and Martill, 2007). The formation consists of four distinct members, though only the lowest Nova Olinda Member yields exceptionally preserved fossils (Martill et al*.,* 2007a). The Nova Olinda Member is a finely laminated limestone, formed authigenically by algae (Heimhofer et al., 2010). The laminae average 1mm in thickness alternating between light and dark blue grey colours when fresh and likely represent wet and dry seasonal cycles. The depositional environment represented is that of a restricted lacustrine or lagoonal setting with a stratified water column. The upper water column was likely brackish and well oxygenated, whereas the lower column and lake/lagoon bottom was hypersaline and anoxic (Heimhofer et al., 2010). More detailed geological and sedimentological information can be found in Martill et al. (2007) and Heimhofer et al. (2010).

3. Materials and Methods

3.1. Collection

Specimens used in this research were donated to the University of Portsmouth by Judith Wohlrabe in 2011. They were obtained via a German fossil dealer and, somewhat ironically, given to Ms. Wohlrabe on account of their perceived poor quality and lack of aesthetic appeal. They were made available to the senior author and assigned new research numbers. Some of the specimens were subjected to destructive analysis and no longer survive, but photographs of them are included within the text nonetheless.

The collection is dominated by specimens of Blattodea (cockroaches), but also includes examples of Orthoptera (grasshoppers and crickets), Odonata (dragon- and damselflies), Hymenoptera (wasps), Hemiptera (true bugs), Diptera (flies), Neuroptera (lacewings and antlions) and Coleoptera (beetles).

Ninety two specimens were studied for this analysis. The majority of unprepared specimens were stored in sealed plastic containers and specimens prepared for SEM viewing were either stored in desiccators or secured by foam in sealed plastic containers with cobalt chloride granules.

3.2. Preparation Techniques

Many Crato Formation insects are damaged by the quarrymen collectors who routinely rub the specimens to 'clean' them, often severely damaging the exposed surface. Consequently, all specimens were initially examined under a light microscope for subjective evaluations of their quality of preservation. The unexposed surface of the insect adjacent to the limestone usually remains pristine. Consequently to examine the unadulterated surface we transferred the specimens to resin blocks (Walton, 1923; Cridland and Williams, 1966; Escapa et al., 2010).

Several techniques were used to prepare the insect specimens. In some cases, a simple wash with water was sufficient to reveal details of the specimen for light microscopy. In some examples excess matrix was removed using fine needles under the microscope. For examination by electron microscopy we employed three techniques: hydrochloric or acetic acid wash to expose the specimen on the limestone slab; acid transfer onto resin blocks, and in some cases the complete removal of the fossil from the matrix using acids. Specimens that were acid etched or completely digested were done so with 10% acetic acid or 5-10% hydrochloric acid, depending on their degree of weathering.

Photomicrographs were taken using an Olympus SZ-STS light microscope with a mounted Nikon DS-Fi1 camera and a Nikon Digital Sight attachment. Images were saved as JPEG files and are either 1280 x 960 or 2560 x 1920 pixels.

Two scanning electron microscope units were used for this project: a JEOL JSM-6100 Scanning Microscope and a JEOL JSM-6060LV Scanning Electron Microscope. Specimens were prepared by mounting on aluminium stubs with a black carbon pad or carbon cement (Conductive Carbon Cement Leit-C). They were then cleaned with a soft squeeze blower and/or acetone to remove any grease and dust. Any remaining gaps between the specimen and the stub were sealed with additional carbon cement and finally they were sputter coated with a gold-palladium alloy using a Quorum Q150RES Sputter Coater. Images were captured and analysed using PC digitiser and 'SemAfore' software. Image manipulation and construction of illustrations was performed using CorelDRAW X5 and Corel Paint-Shop Photo Pro X3.

3.3 What do we mean by exceptional preservation?

If we assume that at the time of death an insect is in pristine condition (but we accept that it may not be), the taphonomic pathway leading to its burial and subsequent diagenesis may result in significant morphological information loss. Thus, as physical damage and decay occur, the condition of the specimen deteriorates. Some Crato Formation insects at macro level appear to be in an excellent state of preservation (e.g. Fig. 2, A and B) and may appear complete with wings, limbs and other appendages intact. On the other hand, there are many examples of Crato Formation insects that are incomplete and are represented by partial examples with one or more wings, limbs or appendages missing. Some wings may show *in-vivo* damage, perhaps attributable to predation, while some appear damaged, perhaps due to prolonged decay. Such incomplete specimens are not necessarily considered to be poorly preserved, but rather, simply reflect the taphonomic state of the specimen on arrival at the site of burial. Our investigation of such specimens often shows that their preservation is remarkable at microstructural levels. By contrast, some complete specimens that appear to be exceptionally well preserved may not reveal detail at microscopic levels (e.g. Fig. 3, A and B), often appearing amorphous under SEM.

In a similar vein, many Crato Formation insects appear to be flattened on the bedding plane surface. However, in reality they are mostly restricted to a single lamina and may exhibit varying degrees of three-dimensionality within the lamina. Indeed, some appendages, especially limbs, may lie at a high angle to the plane of bedding (Fig. 4, A), suggesting submersion in somewhat soupy substrates (*sensu* Martill, 1997).

In addition to the preservation of the exoskeleton, we have discovered several specimens that have internal, non-sclerotized anatomy preserved. In particular we have noted the preservation of muscles and genitalia (see below) beneath preserved cuticles where the specimens have been damaged to expose internal surfaces.

We consider that a specimen is exceptionally well preserved if it displays fragile morphological structures, detail at the cellular level or smaller and the preservation of colour. This can include preservation of fabrics brought about by decomposition and other taphonomic process. Exceptional preservation in the Crato Formation insects includes the preservation of cuticular structures (e.g. scales, setae, sulci, pits, tubercles, carinae), though not necessarily the original cuticle; morphological detail at the micron and possibly macromolecular level, as well as preservation of labile soft tissues with similar degrees of fidelity.

4. Results

The preservation of Crato Formation insects is truly exceptional for non-amber fossil insects. Below we present descriptions and images of the preservation at various levels of magnification documenting macro-, micro- and ultrastructural detail. Our studies show that the preservation can be variable between specimens or even within a single specimen and is in part controlled by the taphonomic state of the specimen at its time of burial/diagenesis.

4.1. Fossilization

The Crato Formation fossils are most commonly encountered as goethite (limonite) replacements of original cuticle. This appears as an orange to brown seemingly amorphous material that is friable and can be easily damaged by touching the specimen. This style of preservation is mostly encountered in the weathered, buff coloured limestones (Menon and Martill, 2007). In unweathered (blue/grey) Crato Formation limestone the fossils are usually black, and more delicate. The former is a weathered version of the latter, whereby the original replacement mineral, probably an iron sulphide phase with carbonaceous material, has been oxidised *in situ* over a prolonged period, perhaps in the last few thousand years. There are examples of specimens that appear to be a halfway stage between these two preservation states.

Non-cuticular soft tissues, such as muscles, are preserved as replacements by apatite minerals (Menon and Martill, 2007). Biofilms surrounding some Crato Formation insects are preserved as silica replacements.

4.2. Macro-Structure Preservation

In both hand specimen and when viewed under a light microscope, it becomes immediately apparent that the Crato Formation insects display a level of preservation worthy of detailed study, and providing a degree of morphological detail rarely seen in fossil insects preserved in limestones or clastic lithologies. Crato insects are commonly complete (abdomen, thorax, head, appendages and wings articulated), often non-compacted with significant 3-dimensionality (Fig. 4, A and B) and commonly reveal colour patterns (Fig. 5, A–D; also see Heads et al., 2005). Internal soft tissues are not necessarily obvious in hand specimens unless the cuticle has been removed when the rock was split. Most Crato Formation insects reveal details of the head and head appendages (preservation of the antennae, eyes and mouth parts is common), the thorax with wings or elytra (usually displaying well defined venation or ornamentation), abdominal segmentation and structures associated with the terminalia such as cerci, ovipositor, caudal gills and other filaments. It is often possible to see spurs, spines and larger setae on limb appendages. These can be preserved intact and perpendicular to bedding (Fig. 4, C–E), while other structures are so well preserved they are nearly indistinguishable from modern counterparts (Fig. 5, E and F).

4.3. Micro-Structure Preservation

Hear we illustrate structures that are only clearly visible under light and electron scanning microscopy (< ~250 µm). The finer details visible at higher magnification demonstrate that the fidelity of preservation of the Crato Formation insects is far better than might be expected from fossils preserved as oxidised replacements. Fine details of exoskeletal structures include individual cuticular scales (Fig. 6, A–H), setae (Fig. 7, A–H), ommatidia (Fig. 8, A–H) and cuticular surface 'ornament' (Fig. 4, D and E). Such structures are often intact and numerous.

The softer tissues like muscle fibres, genitalia and gill structures (that would be expected to decay within hours of death) preserved in phosphate may also display high fidelity (Fig. 9, A–F; Fig. 10, A–C) despite their considerably lower preservation potential (Briggs et al., 1993).

4.4. Ultra-Structure

Here the term ultra-structure refers to the finest details seen within the cuticle or other soft tissues, including muscle fibres, cuticular laminae and micro-papillae. At high magnifications a number of distinctive features are apparent on cuticular surfaces, some of which have a regular appearance and resemble biogenic features that are part of the original cuticle (Fig. 11, A) In general the cuticle appears massive in cross-section with internal laminae only rarely visible (Fig. 11, F). In some cases fabrics found within the cuticle at high magnification may represent the morphology of the preserving minerals, rather than the ultra-structure of the insect (Fig. 12, A and E). Frequently seen ultra-structures within the cuticle include hollow spherical or semi-spherical bodies somewhat resembling pyrite framboids and pyrite pseudoframboids (Fig. 12, B, C and F), both of which we regard as preservational fabrics and are described below. More problematic are spherical aggregates of crystallites arranged in a spiral fashion (Fig 12, D) which have never been described previously as a mineralising fabric. Similarly, they have never been reported for Recent insect cuticle.

Ultra-structural detail on the surface of the cuticle is apparent on some ommatidia, including densely distributed micro-papillae with diameters of ~100 nanometres (Fig. 11, B). Some cuticle displays micro-setae, some of which appear to be hollow at their base and have diameters of 0.5 microns (Fig. 11, A). Similarly, some very small setae display on their external surface patterned fine ridges with widths of ~300 nanometres (Fig. 11, C and D). On rare occasions, ultra-structural detail of internal contents may be preserved with exceptional fidelity (Fig. 11, E). In addition to the above, we have also observed an open meshwork comprising elevated ridges delimiting numerous subquadrate “cells” on the head capsules of elcanid orthopterans (grasshoppers) (Fig. 13 A–F). This meshwork pattern is present on the posterior region of the vertex and on the genae. While the identity of these structures has yet to be confirmed, their position above other cuticular elements strongly suggest that they are epicuticular in nature and may correspond to similar mesh-like structures found in the cement and wax layers of modern orthopteran epicuticle. This feature has not been observed on any other insect cuticle in this study.

4.5. Ultra structure vs preservational fabric

Some features with a regular morphology may better be interpreted as preservational fabrics produced during the fossilization process. In particular, a range of spherical, or subspherical bodies that superficially resemble coccoid microbial bodies are most likely mineralisation fabrics, especially botryoidal and framboidal fabrics typical of pyrite, and possible microbial fabrics of autolithified bacteria or fungi (Wuttke, 1983; Frey and Martill, 1995). Note that some of the autolithified bacteria described by Frey and Martill (1995) in a fossil feather from the Crato Formation have been re-interpreted as melanin bodies by Vinther et al. (2008). Although these fabrics do vary, a framboid-like fabric dominates and is present in almost every specimen. These cylindrical to spherical crystal aggregates somewhat resemble oxidised pyrite framboids (e.g. Berner, 1970) or pyrite pseudoframboids of Ohfuji and Rickard (2005) (Fig. 12, A–F). Significantly however, the spherical objects occurring within the Crato Formation insects appear to be hollow, and thus differ from normal pyrite framboids or pseudoframboids. No such structures have been observed within extant insect cuticle and we here consider they are of either diagenetic origin or may, in some examples, represent autolithified microorganisms.

These hollow spheres vary in size between 1µm and 20µm diameter and are composed of aggregated cryptocrystalline clusters arranged in a weakly laminar fashion, or needle-like crystals arranged in a radial fashion around the hollow sphere (Fig. 12, B; Fig. 10, E). In rare cases, it appears that the hollow spheres have formed between two parallel surfaces resulting in an unusual circular pattern (Fig. 10, F). In some instances the hollow spheres appear to be merged into larger globular aggregates (Fig.10, D).

4.6. Preservational Minerals

The Crato Formation insects are preserved in a variety of mineral phases. The majority of specimens in museum collections are brown or orange-brown coloured goethite replacements of the original cuticle. Soft tissues such as muscle are preserved as replacements in apatite minerals, and while the precise mineral species has not been determined, it is most likely francolite. Unweathered specimens appear black and are probably preserved as amorphous iron monosulphide or perhaps the crystalline forms mackinawite and greigite. Pyrite and marcasite may also be present. Overgrowths of pyrolusite dendrites occur rarely around some insects (Menon and Martill, 2007), while silica, calcite and barite may fill voids within uncrushed specimens.

5. Discussion

Preservation of Crato Formation insects can be extremely variable and the causes of this variation are an important aspect of the formation’s taphonomy. The Crato Formation insects display a spectrum of preservation styles ranging from near perfect examples that appear to have ‘died yesterday’ to specimens that may have undergone considerable biodegradation before being preserved. The preservation allows fine detail to be observed, sometimes at the nanometre scale, but some very fine features within the cuticle may be artefacts of mineralisation. Nonetheless, the fine detail can enable the identification of features of value for taxonomic and phylogenetic studies. Until now, such fine detail has largely been ignored by systematists working on the Crato palaeoentomofauna. While we accept that there may be a reluctance to prepare specimens for routine SEM analysis involving coating with conductive materials, or a fear of risking the integrity of a specimen undergoing acid digestion, we strongly urge workers to consider using these techniques, especially if multiple specimens are available.

Despite this variation, there does not appear to be any taxonomic bias influencing preservation. It is well known that large insects with heavily sclerotized cuticle (e.g. many Coleoptera and some Blattodea) have increased preservation potential resulting in a bias towards larger, more durable insects in fossil assemblages (Martínez-Delclòs et al., 2004; Smith et al., 2006). Unusually, we see both small insects and fragile insect structures (see Fig. 2, B) preserved with astounding fidelity (Barling et al., 2013). This indicates that size and robustness are not controlling factors of preservation in the Crato Formation.

Although the precise geochemical conditions giving rise to this unbiased preservation are still poorly understood, the formation of pyrite and other iron sulphides is usually attributed to the presence of sulphate reducing bacteria (Berner, 1985) and high fidelity preservation in other localities is frequently attributed to benthic microbial communities (Wilby et al., 1996). Although there is a general lack of physical evidence for a benthic microbial community in the Crato Formation (Heimhofer et al., 2010), Heimhofer and Martill (2007, fig. 4.4 a, b) and Martill et al. (2007b) figure ripple-like microbial mats, some with tears for some bedding planes. These suggest that at times extensive benthic microbial communities were present in significant numbers to bind the sediment, and may have influenced fossil preservation.

The preservational textures seen in the cuticle of insects from the Crato Formation presents a unique challenge in determining the process of fossilisation. The cylindrical to spherical aggregates may be the result of failed pyrite framboid formation within the cuticle or could perhaps be artefacts generated by the macromolecular fabric of cuticular laminae as iron sulphide diffused through the cuticle, or a combination of both.

Somewhat similar textures are reported by Wang et al. (2012) in the Early Cretaceous Jehol Biota. These textures differ in three key aspects, but may represent a similar geochemical origin. They differ in that they are on a much coarser scale, are made of discrete, but poorly ordered crystals (more accurately representing pseudoframboids), and do not directly replace the cuticle surface.

There remains considerable work to be undertaken to understand fully the diagenetic environment under which the Crato Formation insects were preserved, but the exquisite preservation is clearly a combination of early diagenetic, microbially induced mineralisation, later *in-situ* weathering, and of course, the keen eyes of the Crato limestone quarry men.

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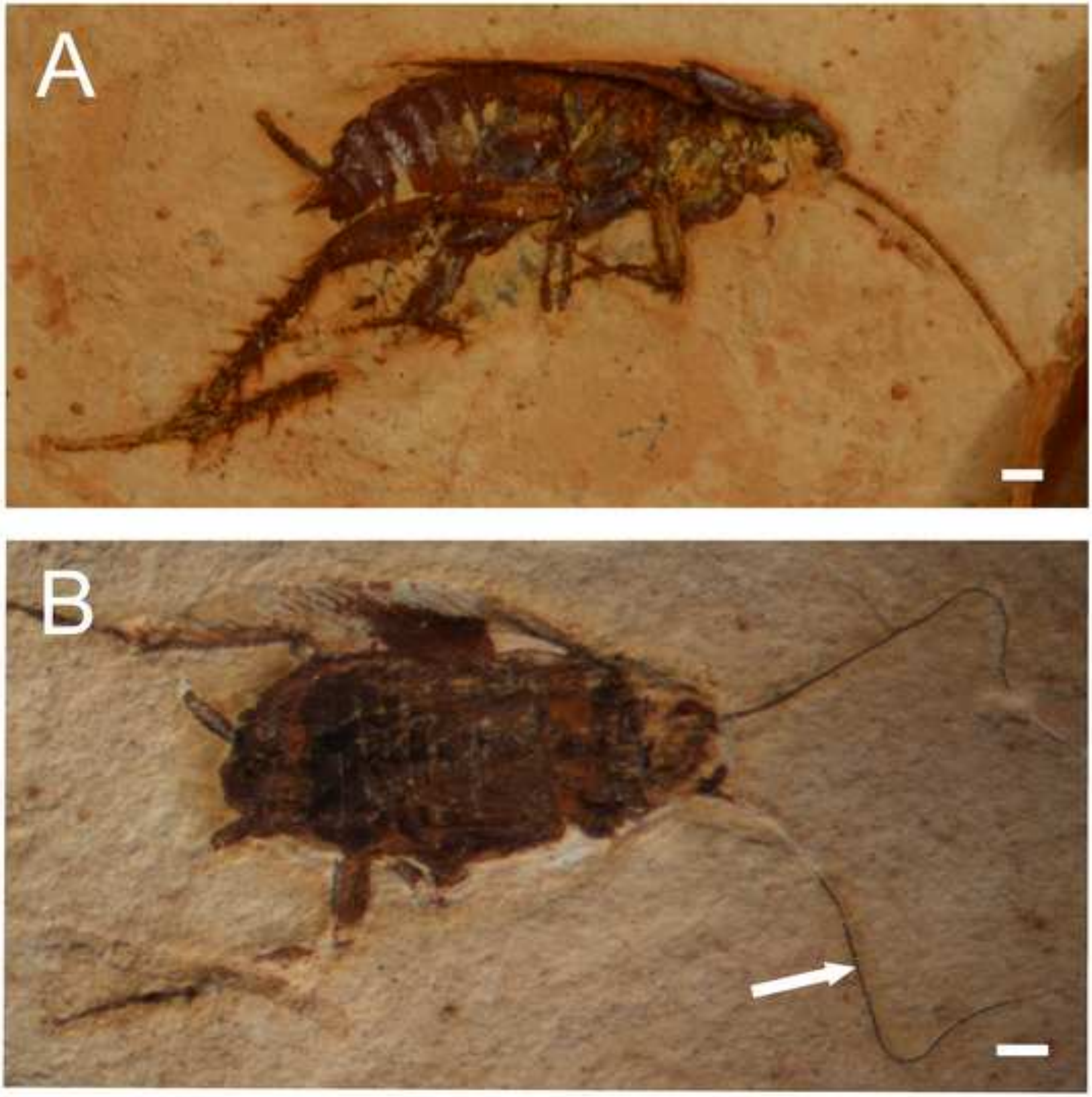

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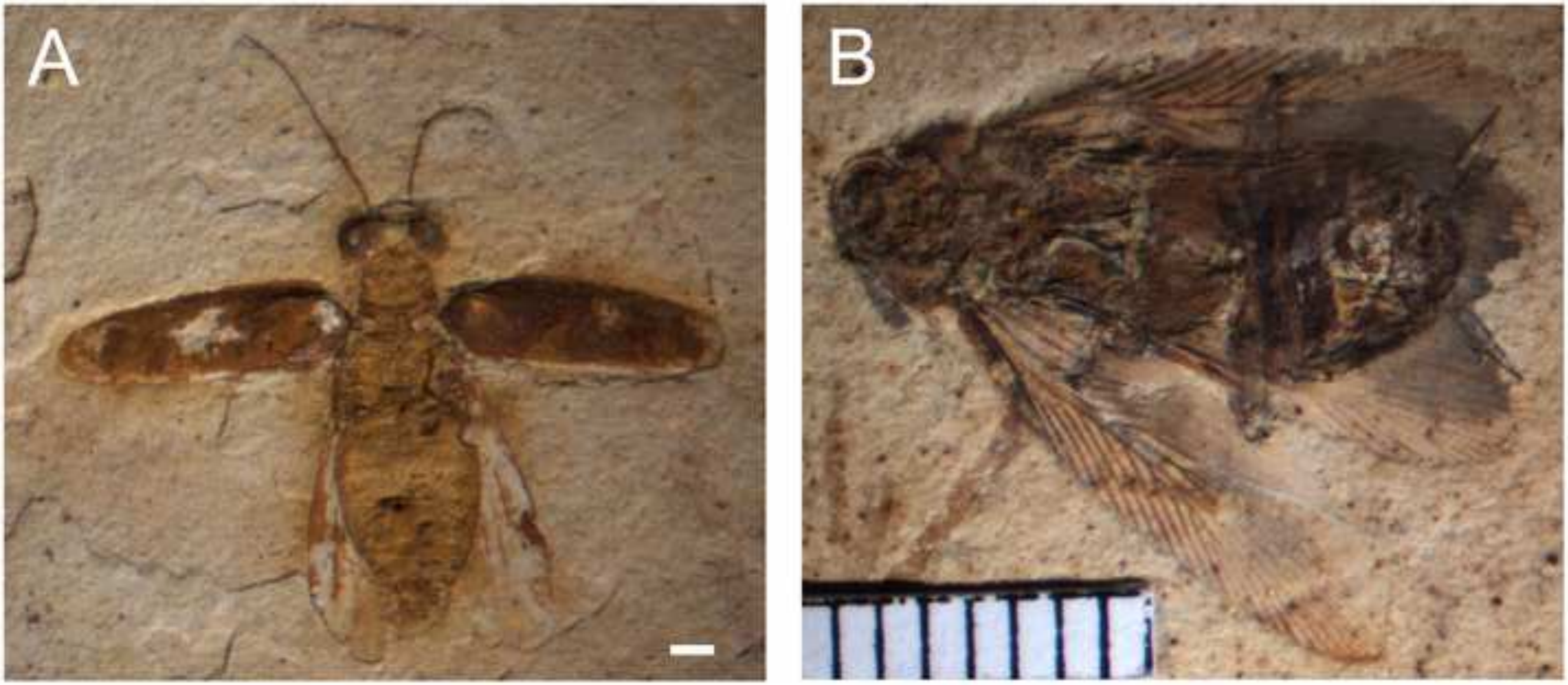

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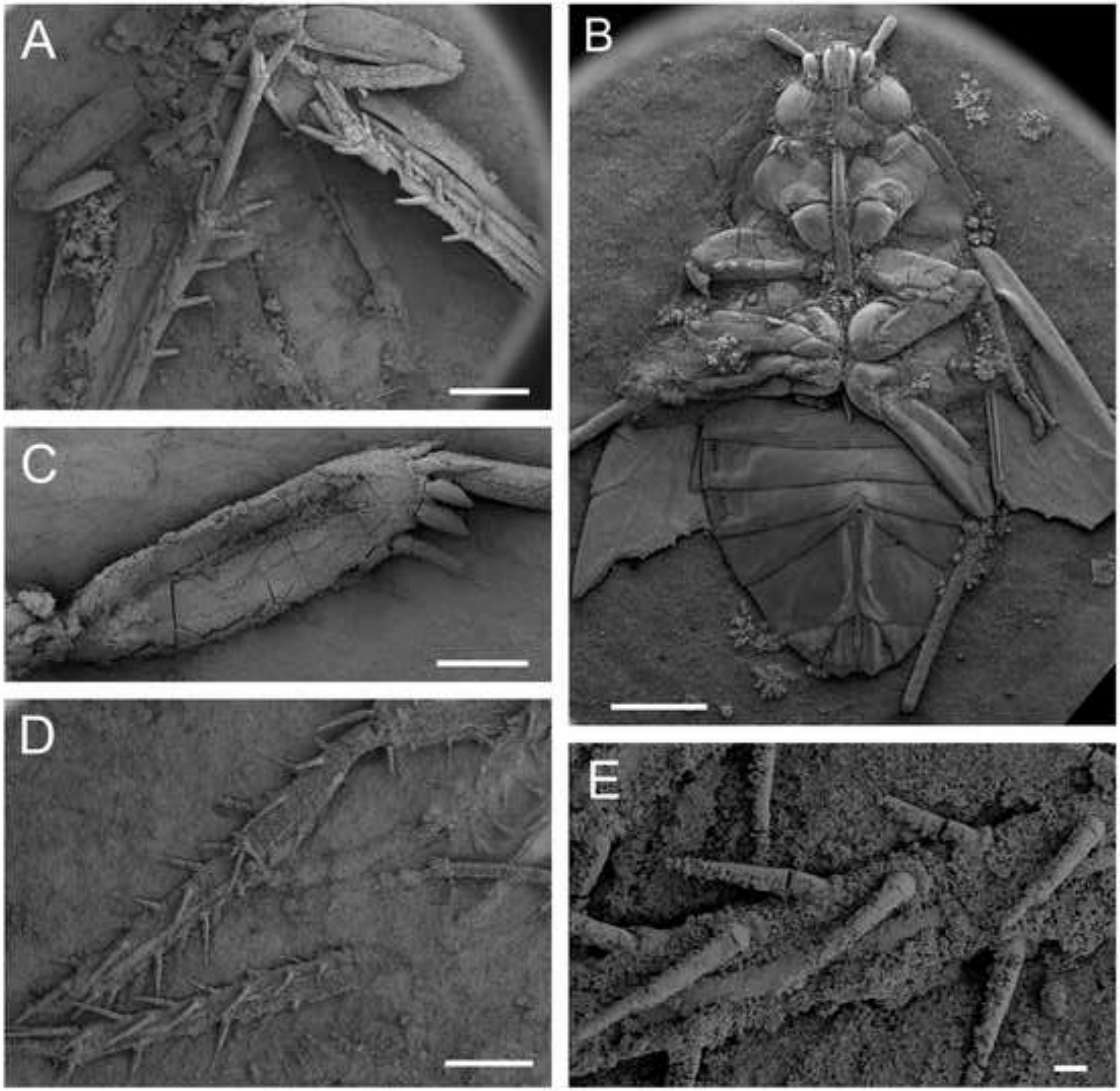

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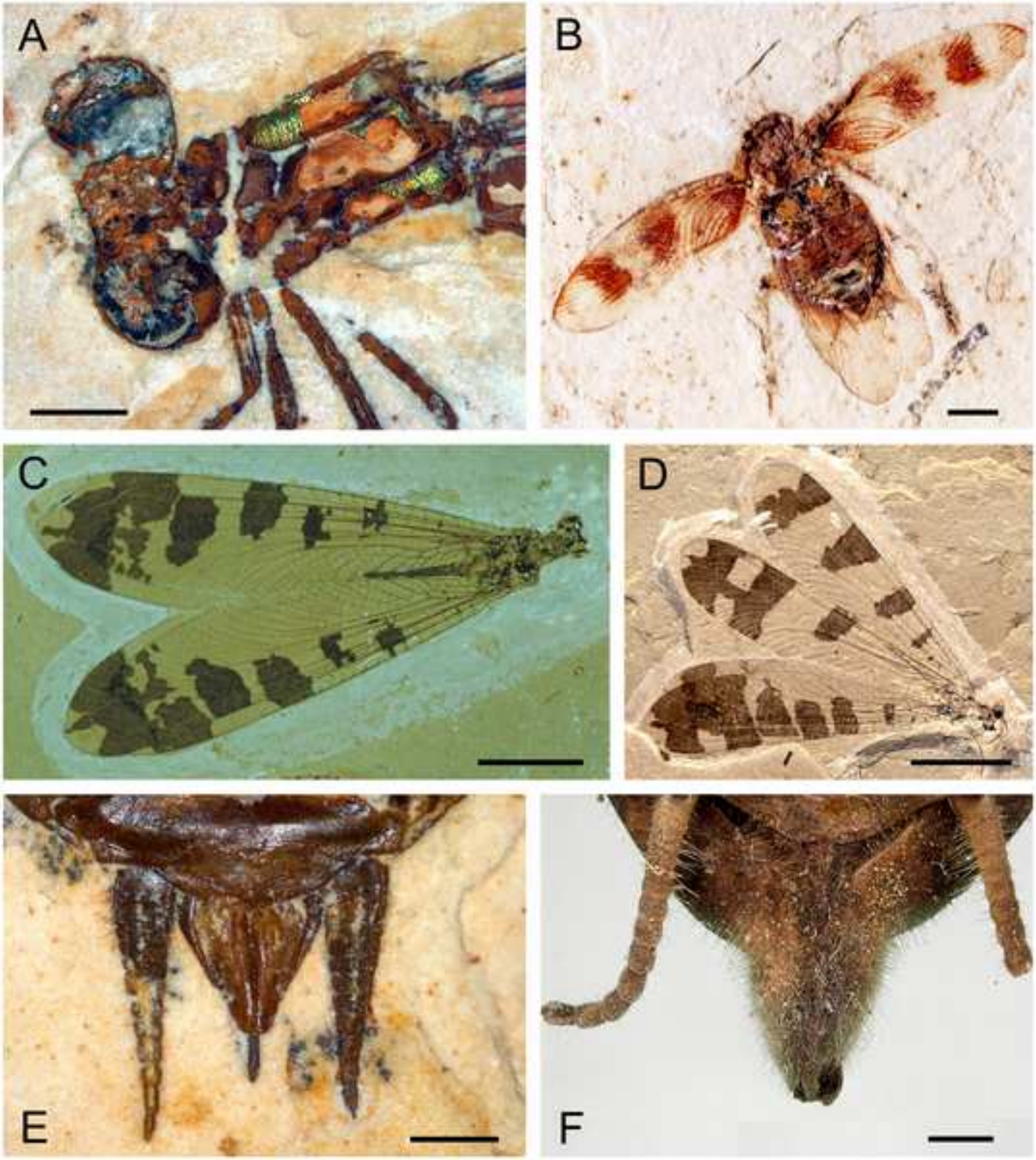

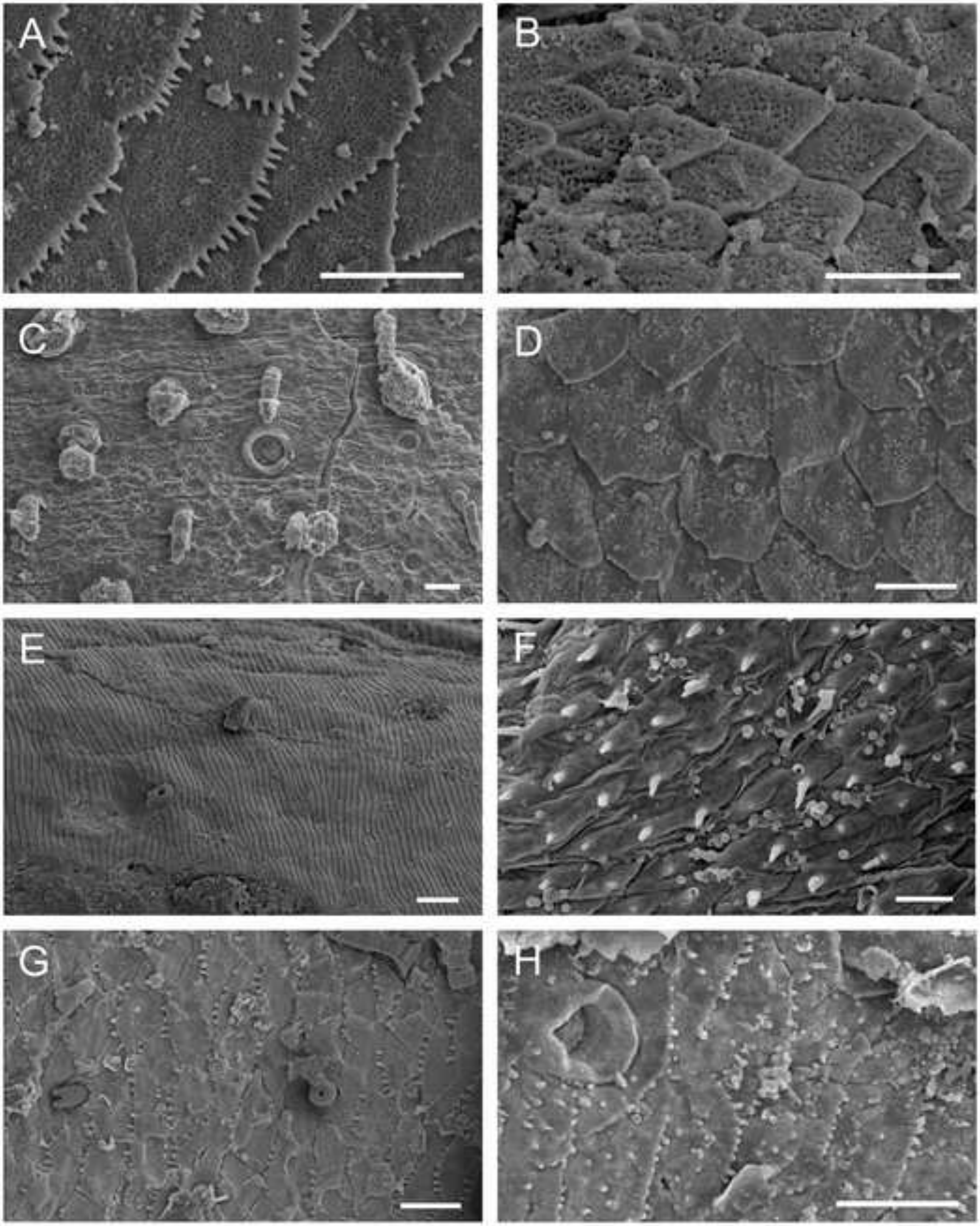
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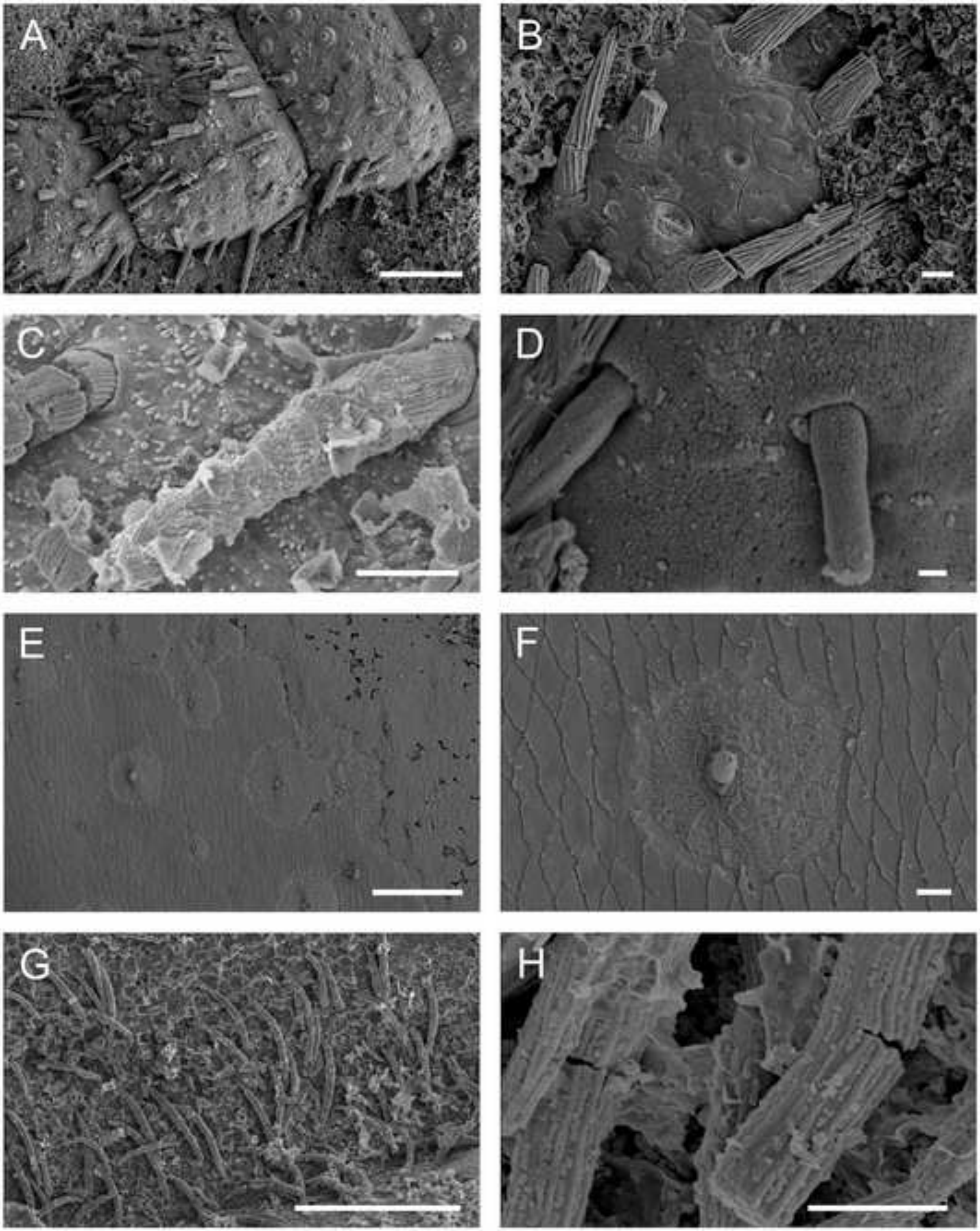

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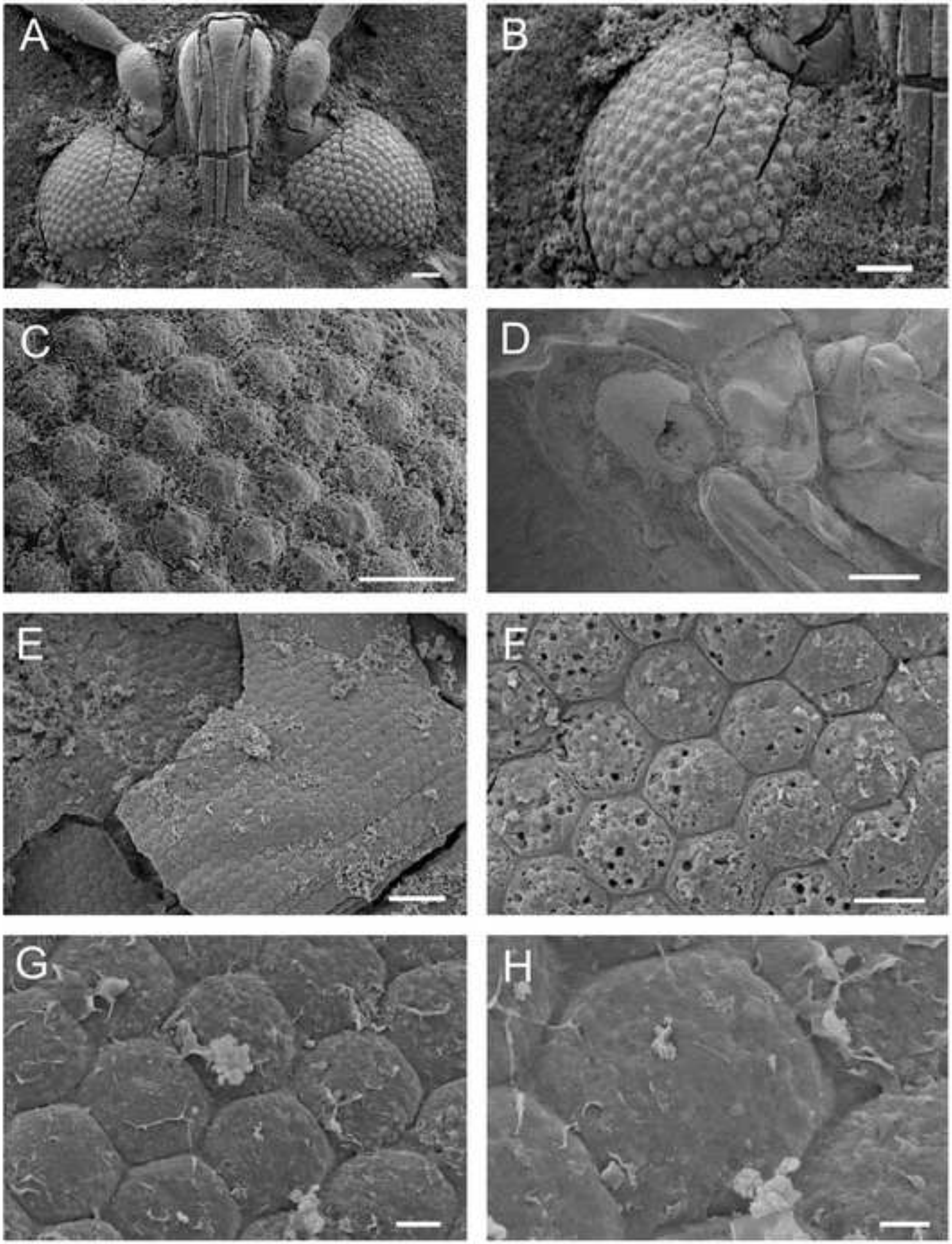

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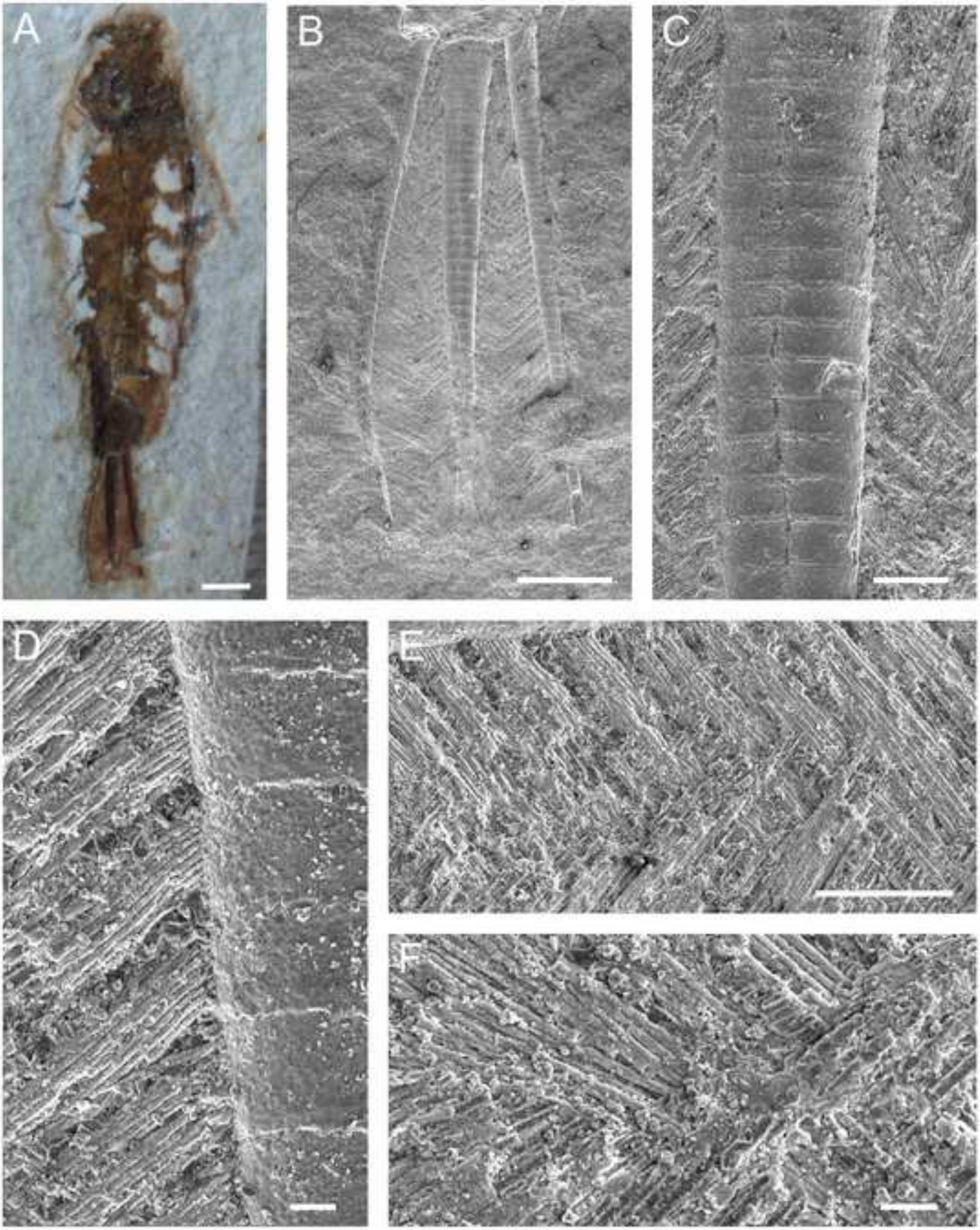

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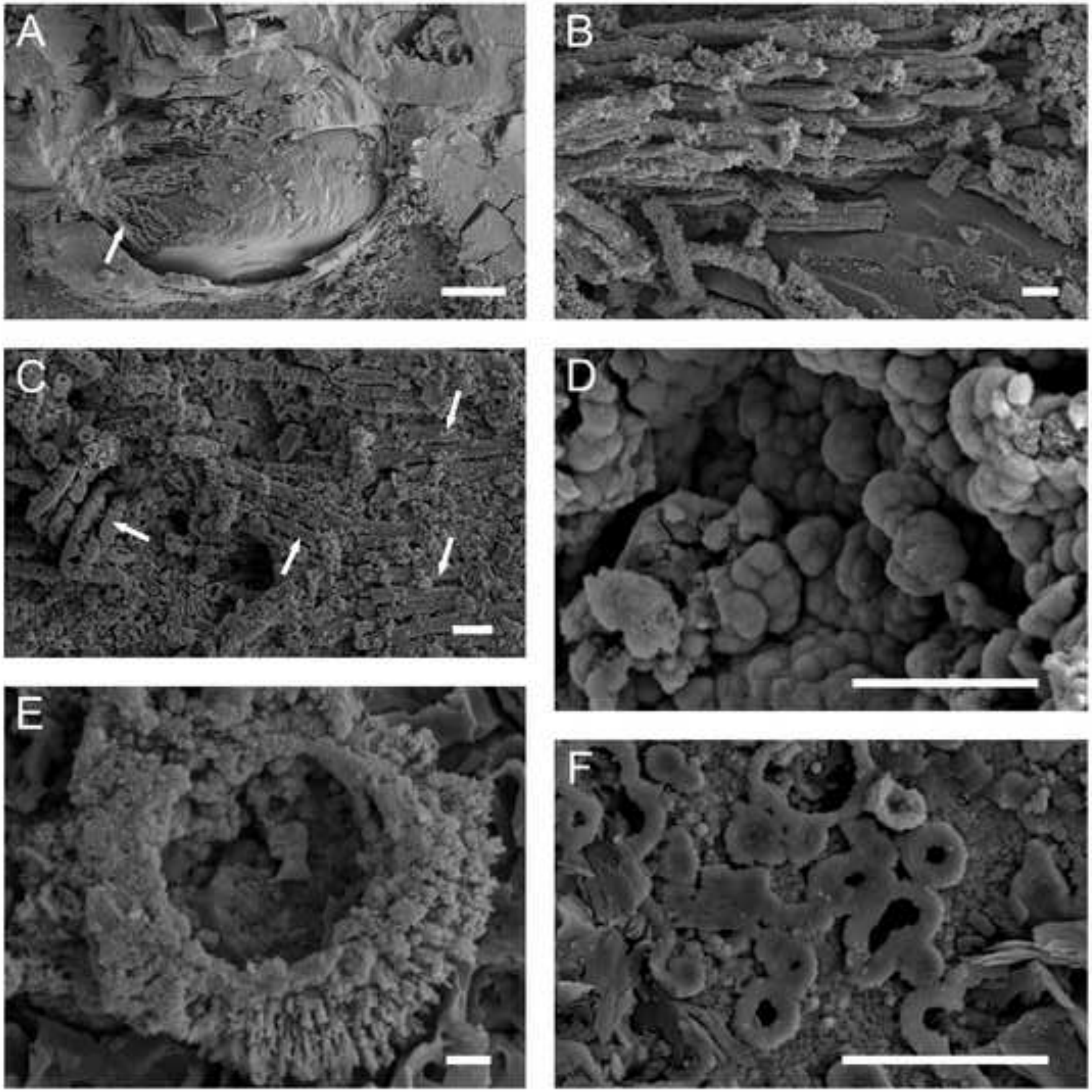

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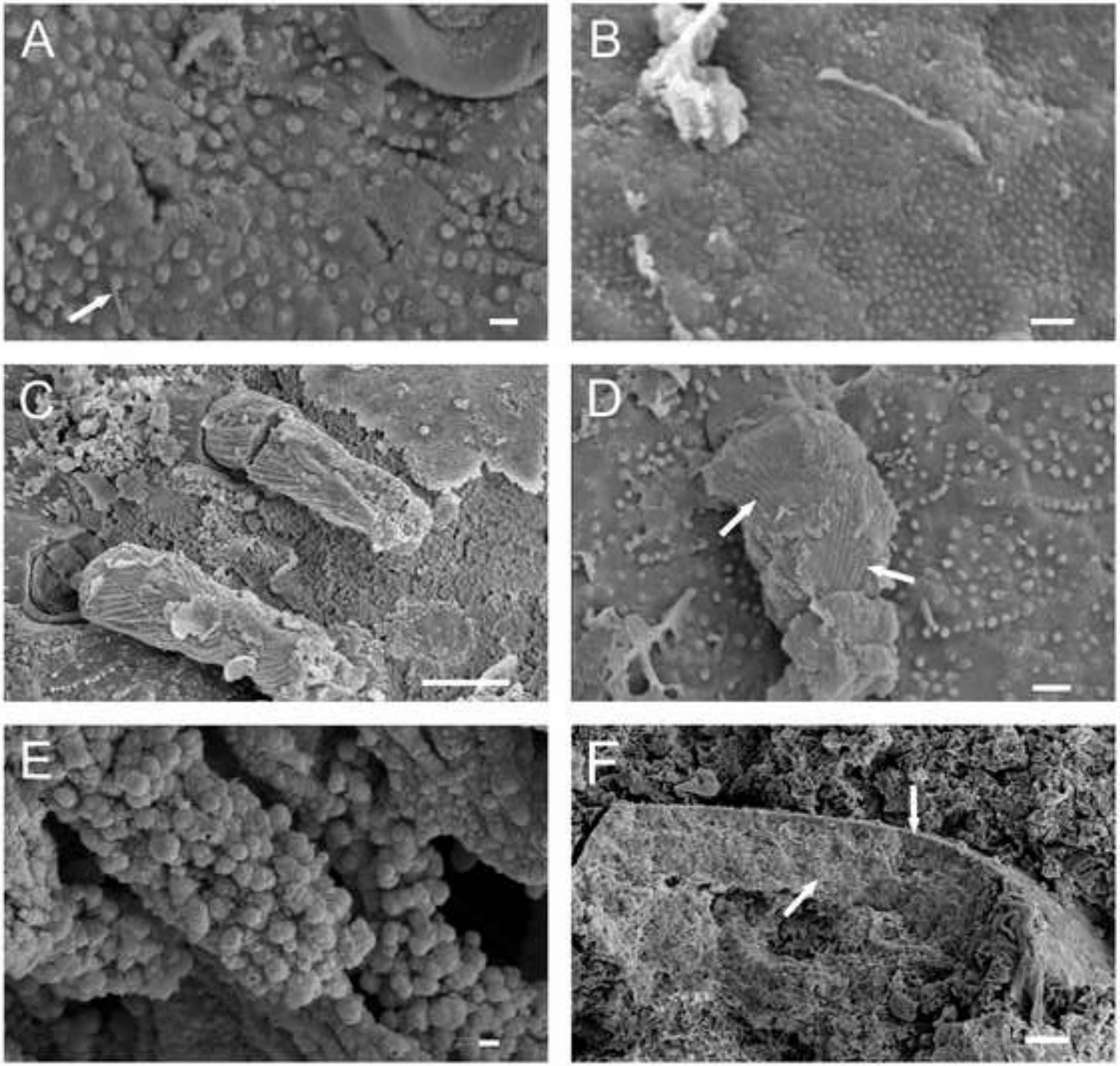

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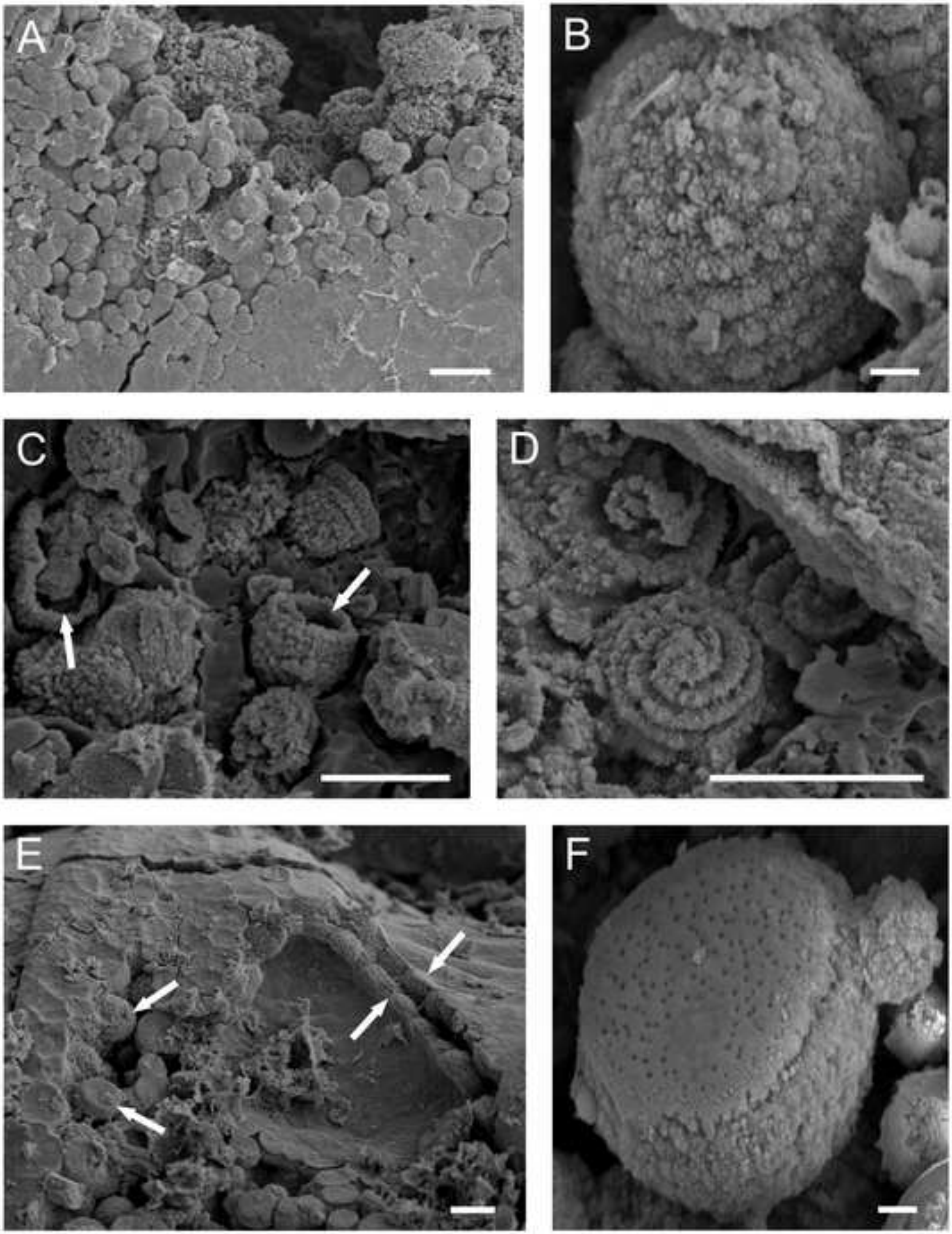

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